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The Pegasus Review: UCF Undergraduate Research Journal (URJ)

Volume 10 | Issue 1

Article 4

2019

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Recommended Citation

Domitz, Ryan (2019) "Grooming Solicitation & Hierarchy in *Cercopithecus petaurista*," *The Pegasus Review: UCF Undergraduate Research Journal (URJ)*: Vol. 10 : Iss. 1 , Article 4.
Available at: <https://stars.library.ucf.edu/urj/vol10/iss1/4>

Grooming Solicitation & Hierarchy in *Cercopithecus petaurista*

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ABSTRACT: Allogrooming is a behavioral adaptation present in many primate systems that serves to organize social hierarchies and promote social cohesion by placating future agonistic conspecifics. Lesser Spot-Nosed Guenons (*Cercopithecus petaurista*) are one species that exhibits allogrooming both in the wild and in captive populations. In a population of *C. petaurista*, dominant males perform proportionately less allogrooming than do females, possibly indicating dominant individuals are the recipients of higher rates of allogrooming than are subordinate ones. My case study catalogs the activity budgets of three captive Lesser Spot-Nosed monkeys and investigates the relationship between allogrooming, solicitation of allogrooming, and aggression. It also examines whether or not these activities can be quantified as metrics for measuring hierarchy. Consistent with the literature, I found no association between allogrooming and aggression. Instead my study supports a positive correlation between aggression and grooming solicitation as a metric of hierarchy.

KEYWORDS: Primate; biology; behavior; grooming; *cercopithecus*; allogrooming; hierarchy

INTRODUCTION

Behavioral variation among primates, in concert with the effect captivity has on natural behavior, can interfere with the interpretation of a species' behavior. Wild populations can sometimes be difficult to study due to political or logistical difficulties. Therefore, a comprehensive understanding of primate behavior often necessitates both field and captive studies (Strier 2003). Like many primates, members of *C. petaurista* live in complex social groups and exhibit an array of communicative and hierarchal strategies. These behavioral strategies vary across the genus *Cercopithecus* (Nowak & Walker 1999) as well as within the order Primates.

Among behavioral strategies employed by *C. petaurista*, females exhibit a sexual solicitation known as "presenting," which involves approaching a male, turning their hind-quarters towards the male, and simultaneously turning their head back to look at him (Morris, 2006). It should be noted that not all presenting behavior is sexually motivated. Presenting can also act as a greeting used to reduce aggression and is most commonly expressed by individuals of higher rank (Morris, 2006).

Agonistic behaviors known as threat displays involve staring with raised brows and typically the "tense-mouth face," "staring open-mouth face," and "silent bared-teeth face" (Morris, 2006). Some populations also display a head bobbing movement as an agonistic behavior (Central Florida Zoo). Grooming is also a form of socialization in primate groups and may confer social as well as antiparasitic benefits (Chiarelli, 1980). *C. petaurista* practices grooming, but studies have shown close kinship rather than hierarchy is indicative of grooming affiliations and aggressive responses between individuals (Schino, 2001; Chiarelli, 1980). Grooming between conspecifics can often be solicited in the form of lying down in the presence of a prospective grooming partner but does not necessarily initiate allogrooming, although the two may be correlated. There is also evidence that females, which tend to form more long-term relationships with conspecifics, practice more proportionate allogrooming than males do (Chiarelli, 1980). Interestingly, there as yet is no known direct correlation between grooming and aggression an individual exhibits in terms of hierarchy. Instead, subordinate individuals are more likely to perform allogrooming because confusing the identity of a grooming partner is of greater risk to lower ranked individuals; as a result grooming ultimately helps placate future aggressors (Chiarelli, 1980). Thus, individuals

of similar proximity (both geographic and hierarchal) tend to belong to the same grooming associations and have been observed supporting their grooming partner in social conflicts (Chiarelli, 1980). This observation suggests that, in Old World primates, hierarchy is better measured in terms of the power of displacement one individual has over another than in terms of allogrooming received (Chiarelli, 1980). This implication, in turn, makes interpretation of the hierarchal stratum, a task crucial to managing captive populations, difficult. The present study thus asks whether allogrooming, grooming solicitations, and acts of aggression serve to maintain and identify hierarchy within captive populations of *C. petaurista*.

METHODS

Lesser Spot-Nosed Guenon



Figure 1. Tumani grooming herself

C. petaurista live in polygynous social-mating groups called troops, consisting of 10 to 40 individuals (Central Florida Zoo). There is typically one dominant male; however, group compositions can fluctuate and it is hypothesized male numbers can increase due to the selective advantage gained from predator mobbing (Zuberbühler & Jenny, 2002; Nowak & Walker, 1999). Members of the genus *Cercopithecus* are territorial but predominantly avoid conflict (Nowak & Walker,

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1999). Sexual dimorphism within the genus is notable, particularly in body and canine size (Fleagle, 1999). Average weights for females and males are 2.9 kg and 4.4 kg respectively (Fleagle, 1999). Distribution of the species averages 29.3 individuals per km² (Zuberbühler & Jenny 2002). In the wild, *C. petaurista* occupies a vertical intermediate niche within the canopy of its habitat (McGraw, 2000). This species demonstrates relatively specialized niche partitioning amongst primate species such as *C. campbelli* and *C. diana*, both of which share the canopy, and such niching behavior lowers interspecific competition among species (Wachter et al., 1997). Individuals average between 0.91 and 1.22 meters in length and live approximately 20 years in captivity (Central Florida Zoo). The species uses cheek pouches to store small amounts of food while foraging, and this storage method has been shown to decrease the amount of interspecific competition between neighboring and overlapping niched species (Buzzard, 2006).

Enclosure and Individuals

My study took place at the Central Florida Zoo and Botanical Gardens in Sanford, Florida. The guenon enclosure (9.144 x 7.62 x 3.353 meters) has three individuals: two females and one male. Mama, subject A, the oldest, was born in 1999: 18 years old at the time of the study. Timbi, subject B, the only male, was born in 2003: 14 years old at the time of the study. Tumani, subject C, the newly introduced female was born in 2001: 16 years old at the time of the study. It should be noted that Tumani and Timbi are predominantly a mating pair and are half siblings on the father's side. The enclosure has two heating sources for colder days, as well as two exits for feeding.

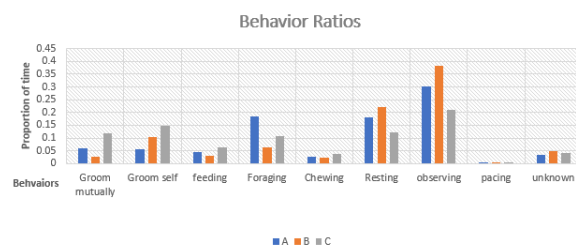
Reintroduction Event

On March 26th, 2017, Mama was removed from the enclosure as a consequence of a fight with Tumani. Following the removal of Mama from the enclosure and her subsequent reintroduction into the captive troop, high levels of aggression were directed at her. The reintroduction event marked a change in behavior particularly from the females, Mama and Tumani.

Approach

The monkeys were observed at random times during the zoo's operating hours between 9:00am and 5:00pm. The observation took place over a period of 34 days for

a total duration of 3376 minutes (mean: 99.3 min per day). Changes in each individual's location and behavior were recorded each minute using a grid and behaviors stereotyped in part from a previous study of the species (McGraw, 2000). Behavioral ratios include the proportion of time spent by a given individual engaged in one of the following behaviors, as reported in Figure 2. Specifically, I compiled and analyzed the behavioral ratios using averages of the time occupied by a given behavior, and divided by the average observation time. I then performed an analysis of covariance (ANCOVA) on the continuous behavioral independent variable, allogrooming, as a function of the dependent variables, grooming solicitation, monkey identification, and pre/post reintroduction. I also used an ANCOVA test on the behavioral independent variable—grooming solicitation—as a function of the dependent variables—pre/post reintroduction, monkey identification, and time observed. In addition, I used a non-parametric Wilcoxon test to compare aggression ratios among individuals before and after the reintroduction event. Lastly, to elucidate behavioral consistency between individuals, I measured the variance of individual behaviors as a proportion of mean stereotyped behavior to calculate the coefficient of variation within each behavior profile.

RESULTS*Figure 2*

The most proportionate allogrooming was exhibited by Tumani, subject C (Figure 2), while Timbi, subject B, exhibited the lowest proportionate allogrooming (Figure 2), which is typical of males (Chiarelli 1980). Consistent with the literature (Chiarelli 1980), most of the grooming associations were between the females, A & C (Figure 2).

Source	Df	F	p<
Grooming solicitation	1,96	0.0921	0.7622
Monkey ID	2,96	10.41	0.0001
Reintroduction	1,96	2.388	0.1255

Table 1. Test for Influence of Grooming Solicitation, ID, and Reintroduction on Allogrooming

The ANCOVA test for influence of monkey identity, the reintroduction event, and grooming solicitation on rates of allogrooming indicate that only monkey identity as a variable influenced allogrooming (Table 1). Neither the reintroduction event nor solicitation of grooming influenced group allogrooming rates, reinforcing the idea that allogrooming and grooming solicitation are not casually related.

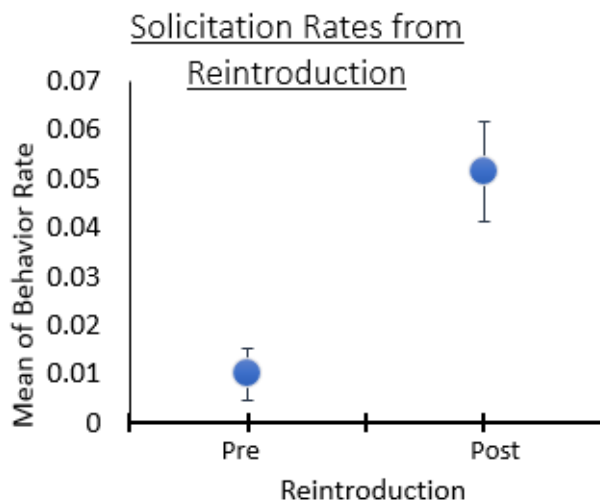


Figure 3

Source	Df	F	p<
Monkey ID	2,96	7.79	0.0007
Total Time	1,96	0.93	0.337
Reintroduction	1,96	12.93	0.0005

Table 2. Test for Influence of Reintroduction, ID, and Time on Grooming Solicitation

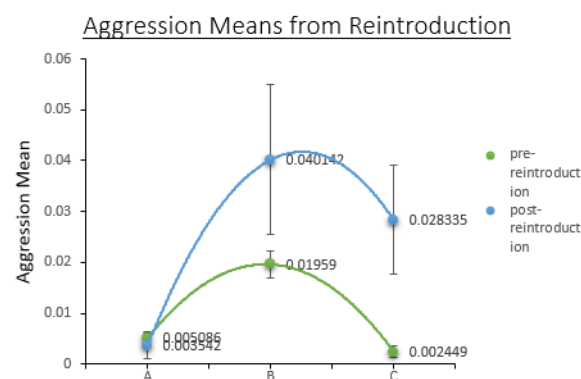


Figure 4. *Pre-* ($X^2 = 32.53, p < .05$) *Post-* ($X^2 = 6.42, p < .05$)

The second ANCOVA test for influence of monkey identity, the reintroduction event, and the time observed, on grooming solicitations indicate that Mama's reintroduction as well as monkey identity influenced grooming solicitation rates (Figure 3, Table 2).

Timbi's (B) power of displacing other individuals within the enclosure (Chiarelli 1980) in concert with his highest proportional counts of aggression (Figure 4) are both indicative of his position as alpha male within the group. This result was expected as Timbi is the sole male of the captive group. The non-parametric Wilcoxon test analyzed rates of aggression before and after the reintroduction event and measured a notable increase in aggression from Timbi and Tumani (Figure 4). Thus, the reintroduction event marked a notable increase in aggression as well as grooming solicitation, supporting the idea that grooming solicitation rates are positively correlated to aggression. This result was not what I expected as I believed that the grooming elicited, rather than solicited, would be a valuable metric to measure hierarchy by.

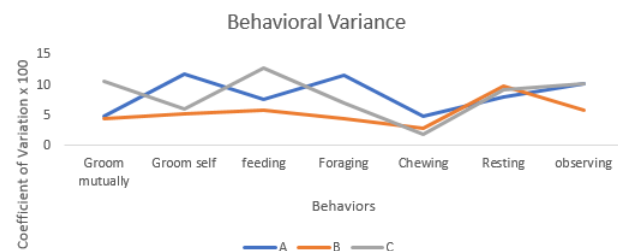


Figure 5

Overall, Timbi (B) reflected a more stable behavior pattern and had the lowest behavioral variance in his activity budget (Figure 5).

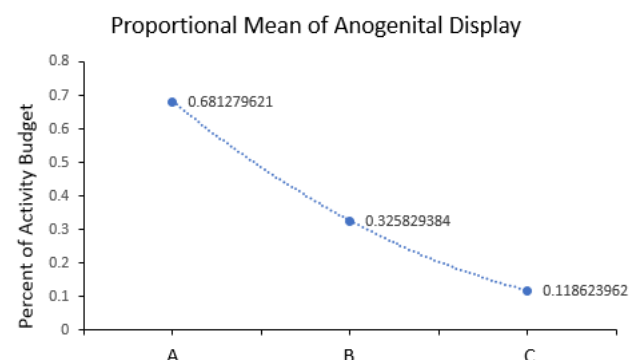


Figure 6

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Another feature of communication between hierarchal individuals involves the presentation of the anogenital region to another individual, most commonly expressed by individuals of higher rank (Morris, 2006). My data, however, did not support this conclusion because Mama elicited anogenital cues in higher frequencies than Timbi or Tumani (Figure 6).

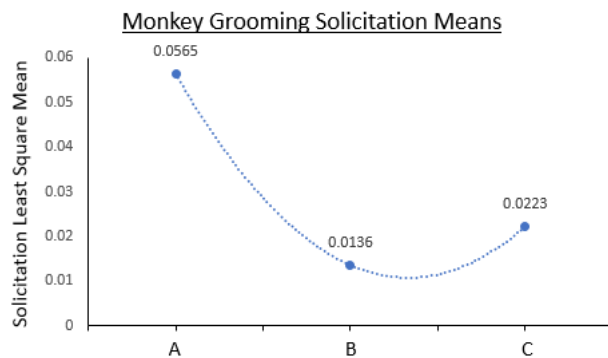


Figure 7

As expected, a higher status individual Timbi (B) elicited the least proportional grooming solicitation, whereas Mama (A) elicited the most (Figure 7).

DISCUSSION

This study demonstrates that grooming solicitation rates in *C. petaurista* are a more accurate metric to measure when studying hierarchy than rates of allogrooming elicited. The reintroduction event served to polarize changes in behavior, in contrast to control behaviors measured before the incident. Prior to reintroduction there was little conflict among conspecifics, and thus no known behavior associated with aggression. After Mama was reintroduced, however, it became clear that the grooming she elicited was not conducive towards placating her future aggressors. Mama's levels of grooming solicitation spiked upon reintroduction in concert with higher aggression exhibited towards her. It should thus be noted that grooming solicitation is a stationary behavior that exposes her further to such aggression.

Allogrooming rather than grooming solicitation was what I expected to be a valuable metric to gauge hierarchy and so the results were contrary to my own prediction that higher status individuals would receive higher proportionate rates of allogrooming. Measuring hierarchy in populations may serve to better understand

group dynamics and to consequently better manage healthy captive groups; this task is particularly important because interpretation of the group behavioral dynamic has the capacity to be skewed due to small group size, captive setting, and any effects from inclusive fitness between half siblings like Timbi and Tumani.

Timbi's low behavioral variance may be reflective of a more stable activity budget as a consequence of his position as the dominant individual within the hierarchy of the group. Timbi is characterized by high aggression rates and low grooming solicitation rates in response to Mama's reintroduction. Timbi and Tumani's spike in aggression in response to Mama's reintroduction occurred conjointly with higher grooming solicitation rates across the enclosure, but not with higher allogrooming rates. This data are my main evidence supporting the idea that grooming solicitation has less of a relationship with allogrooming and more of a relationship with aggression rates.

To sum up, in terms of monkey identity, grooming solicitation and aggression are inversely related. In terms of the reintroduction event, grooming solicitation and aggression rates are positively related. Subject B, Timbi, is the most dominant individual in terms of aggression and solicitation; then subject C, Tumani; and lastly subject A, Mama.

ACKNOWLEDGMENTS

I'd like to thank Dr. Ken Fedorka, Dr. John Starbuck, Frank Logiudice, Emily Dovydaitis, and the Central Florida Zoo for the experience, opportunity, and guidance during the study.

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